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The influence of global climate and hydrography on microbial activity in the ocean: results of a N-S Atlantic transect

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Abstract:

The Atlantic in his longitudinal dimension, stretches over most of the dominating global climatic and hydrographic zones. The aim of this study was to characterize zones of biological activity along a N-S transect through the Atlantic and to see whether these corresponded to well known physical oceanographic and climatic zones. During this transect measurements of chlorophyll, cyanobacteria, actively metabolizing bacteria, protease activities, V_m and turnover rate of easily degradable substances were made in 4 to 24 h intervals. The cruise took place from November 1991 to January 1992, thus an autumn situation in the North could be compared to a spring situation in the South. The results demonstrate, that there is a distinct zonation of the Atlantic with respect to biological activity, which clearly reflects the large scale environmental conditions. All variables showed their highest values in the corresponding northern and southern moderate climate zones. Low values were measured in the two corresponding subtropical zones. In the tropical zone (somewhat smaller than geographically defined), activities increased in comparison to the subtropical zones. Lowest values were nearly always measured in the Antarctic region. Normalized to chlorophyll (representing the food source for heterotrophic organisms), it turned out that most of the relative activities reached their maximum in the tropical zone, whereas in the adjacent northern and southern zones they decreased considerably. This suggests a temperature dependency of heterotrophic activity. However, if the activities are related to water temperature it turns out, that moderate climate zones with higher nutrient supply show high values, whereas activities in the tropical/-subtropical zones are relatively low and more similar to those found in Antarctic waters. This is surprising because these zones cover a temperature range of about 30 °C. It is concluded, that especially in Antarctic waters, nutrient supply and probably enzyme adaptation, are compensating low temperature effects to a certain extent. In the warm region low nutrient supply may be responsible for relative low activity rates.

Keywords:
Atlantic ocean, biological zonation, chlorophyll distribution, inorganic nutrients, ectoenzymatic activity, cyanobacteria, active bacteria.

Introduction

The world ocean, in his huge dimensions, is believed to have a major influence on climate as well as on climate change and vice versa. This can be looked upon from the physical, chemical, biological and hydrographical view point. Biology is one important aspect for the dynamic of biogeochemical cycles in the sea, because organisms mediate between the dissolved, solid and gaseous state of chemical compounds. Organisms regulate organic/-inorganic matter distribution throughout the ocean. Microbial components of the marine biota contribute substantially to these processes, because they penetrate the water most intimately by their high number of individuals, and because they comprise the largest part of total biomass in the sea.

The mixed surface layer of the ocean is directly exposed to atmospheric conditions and therefore the full response of organisms to these conditions can only be investigated there. We made a transect through the Atlantic from about 50°N to 65°S, crossing most of the global climatic and hydrographic zones. Near surface samples were taken in short intervals to gain a satisfactory resolution of the dominant current systems and the microbial activities within them. Microbiological investigations covering such a wide area of the ocean are rare in the literature (Vaccaro et al. 1969, Gordon 1970a, b, Fournier 1971, Kriss et al. 1971, Sorokin 1971, Kriss & Stupakova 1972), and methods applied in earlier studies were not so much developed as they have become in recent years. Modern microbiological methods allow a better insight into metabolic coupling of photoauto-trophic and heterotrophic processes and their individual dynamics, which are closely linked to small scale environmental and large scale climatic conditions (Ducklow & Carlson 1992). These processes have a primary influence on biological CO_2 fixation, simultaneous CO_2 remineralization and export of imbalanced organic carbon, which are the main goals of the international JGOFS-(Joint Global Ocean Flux Study)-program.

For the interpretation of biological data from such a wide area of investigation, the general oceanographic situation has to be taken into account. The main currents in the Atlantic can be attributed to the dominating climate zones. Chemical and physical properties of the currents, which have a bearing on their living biota, are influenced by the climatic regime of the area under observation, but also by the origin of the current, its course and other hydrographical events such as upwelling and mixing. Crossing the currents on a longitudinal transect at about 30°W enabled us to characterize the biological patterns of the different currents, as they resulted from the present climatic and hydrographic conditions.

It was the aim of this study to investigate the influences of environmental factors first on primary producers, and second on bacteria and their decomposition activity. With other words, we wanted to see, whether a latitudinal zonation of the ocean as it is well described for physical oceanographic patterns does also exist with respect to biology. On the basis of our data we tried to demonstrate and to calculate zone-specific relationships between physical/chemical and biological parameters, between autotrophic and heterotrophic parameters, and between bacterial abundance and activity parameters. Furthermore we attempted to present some information on the relative importance of the different zones with respect to their productivity and decomposition capacity. Because the cruise took place from October to December, the seasonal aspect, autumn in the North and late spring in the South, is also involved. Nearly simultaneously, biological observations and comparisons could be made from distinct corresponding regions in the northern and in the southern hemisphere. Our study may serve as a base line for further investigations on biological changes and perturbations due to possible changes of climate.

Material and Methods

All sampling was done while the ship was underway. Temperature and salinity were continuously recorded by the ships automatic registration system. Samples for all chemical, planktological and bacteriological measurements were taken at about 11 m water depth by a continuously running peristaltic pump . Sampling intervals were adjusted to the time needed for processing the water according to the different procedures, usually they were between 4 and 24 hrs. Nitrate, phosphate and silicate were determined with an autoanalyzer, according to standard procedures of Grasshoff (1976). Chlorophyll a was determined fluorometrically after ethanol extraction (5 ml per filter) . Picocyanobacteria (CB) were counted microscopically by their autofluorescence in an epifluorescence microscope (Zeiss Standard, exitation wave length 490 nm, emission wave length >520 nm, magnification 630). Organisms were filtered on 0.2 µm Nuclepore membranes and 25 fields (at least 400 cells) were counted by means of a Pettersson grid to obtain a confidence level of 95 %. All counting was done on shipboard, within a few hours after sampling.

The following bacteriological activity parameters were determined: maximum velocity of glucose uptake by bacteria (V_m glucose), turnover rate of leucine in the water (T_R Leu), number of metabolically active bacteria as detected microautoradiographically by the ^{3}H-leucine uptake of bacteria (MAR leu) and extracellular protease activity of bacteria (EPA).

Maximum velocity of glucose uptake by bacteria was estimated at <u>in situ</u> temperature by ^{14}C-glucose additions to the water at a saturating concentration of 20 µg C l^{-1}. Incubation lasted for 2 - 3 hrs according to the ambient water temperature. After filtration on 0.2 µm celluloseacetate filters, radioactivity in the particles was measured by liquid scitillation techniques. From the results of 3 parallels and 1 fixed control, V_m was calculated in terms of nmol $l^{-1}h^{-1}$ glucose taken up by the bacteria.

For the determination of the leucine turnover rate, ^{3}H-leucine at a concentration of 0.1 µg C l^{-1} was added to the water. Further processing was similar to that of V_{max} determination, however in this case 0.2 µm Nuclepore membranes were used for filtration because of their low adsorption of radioactivity. Turnover rate of leucine was calculated in terms of % d^{-1}, that is percentage of the leucine taken up by the bacteria per day from the actually occurring pool of dissolved free leucine. In detail the application of both radiotracer methods followed protocolls of Gocke (1977).

Numbers of active bacteria in the water were determined by labelling with ^{3}H-leucine (5 µCi ml^{-1}) during a 3 - 8 h incubation period at in situ temperature. Because only few bacteria were expected to be labelled in offshore oceanic samples, bacteria were concentrated on a small spot (3.5 mm diameter) by filtration on 0.2 µm

Nuclepore membranes. For this purpose a special filtration apparatus with 9 microfunnels was constructed (Hoppe unpublished). Subsequent microautoradiographic processing of the filters followed the method of Tabor and Neihof (1982). Silver spots in the X-ray film caused by labelled bacteria were counted in a Zeiss Axioplan microscope at a magnification of 630. From the spot counts of 20 fields or Petterson grid sections the number of metabolically active bacteria per ml water was calculated.

Protein hydrolysis was measured via extracellular protease activity (EPA) using the fluorogenic substrate analog Leu-MCA (Leucine-Methyl-coumarinylamide) as described by Hoppe (1983, 1993). Substrate concentrations ranged from 0.1 to 100 µM and the incubation time at in situ temperature was between 4 and 12 h. Incubations were made in 1 cm polyethylen cuvettes of the 1/2 micro type. These cuvettes were also used to determine the fluorescence arising from the hydrolysis of the substrate analog which results in the liberation of the fluorochrom Aminomethylcoumarin (AMC) from the combined molecule. Settings of the fluorometer (Kontron SFM 25) for time series of fluorescence measurements were 354 nm for exitation and 445 nm for emission wave lenght. Four parallels were run at each substrate concentration. Fluorescence readings were calibrated by standard additions of a suitable AMC standard solution. Fluorescence increases per time were converted to values of leucine liberation from the substrate analog and from these values the velocity of carbon liberation was calculated in terms of $V = \mu g\ C\ l^{-1} d^{-1}$.

The cruise plan

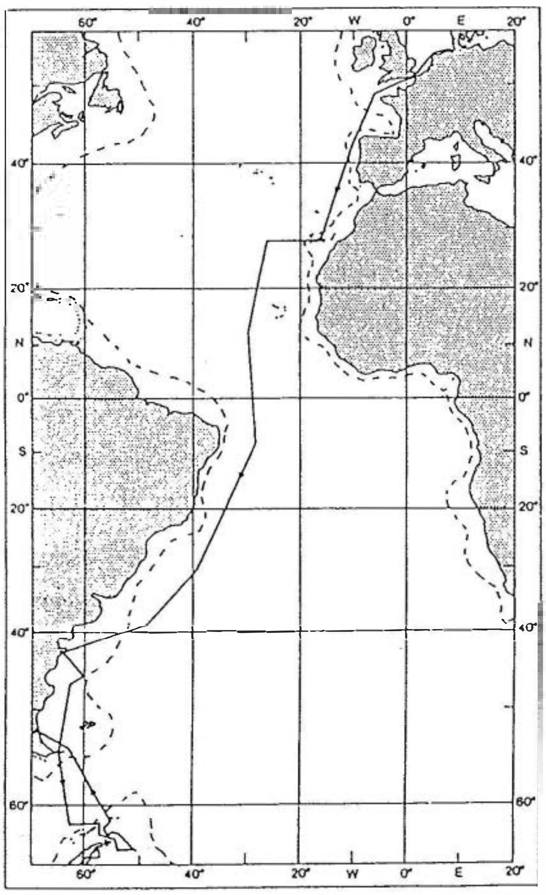


Fig. 1: Map of the Polarstern cruise from 14th Nov. 1991 to 2nd Jan. 1992. The continental shelf is roughly indicated by the dashed line.

The Polarstern cruise X leg 1a/b took place from Nov. 14th, 1991 to Jan. 2nd, 1992. It's course is mapped in Fig. 1. The cruise started in the North Sea (53°53'N/8°70'O) and reached it's most southern point off the Antarctic peninsula (62°15'S/53°00'W). With respect to climate and its consequences for life cycles in the ocean we were able to trace an autumn situation in the northern hemisphere and a spring situation in the south, and to compare these two situations with each other. The ship left the continental shelf west of Britany (48°N, 7°W), then it went straight on to the Canarian Islands (Teneriffa). In the northern and southern subtropical areas and in the tropical area it followed a course roughly along the 30th degree of longitude. In the south, the ship entered the continental shelf area at about 40 S/56°W to reach the Argentine harbor Puerto Madryn. From there it went strait on southward across the Patagonean shelf to the Antarctic region. The Patagonean shelf area was left at 56°S, 65°W. The influence of the different hydrographic currents and climate zones, which were crossed on this N-S transect, on biological parameters is discussed in detail after presentation of the results.

Results

Salinity and temperature (Fig. 2): Salinity showed a remarkable variability on this Atlantic transect, which reflected most impressively the hydrographical and climatic regime. Salinity was comparatively low in the North Sea region, due to low evaporation and high freshwater input by rivers. It increased steadily in the subtropical latitudes. In the tropics from 20°N to 20°S salinity decreased considerably, reaching its minimum at 10°N. This is the region of the equatorial currents and countercurrent system, where heavy rainfall, mixing of surface water with low salinity intermediate water in divergent zones and/or currents originating from low salinity coastal waters may cause a salt reduction in the surface layer. In the South Atlantic the drastic decrease of salinity south of 40°S was the most obvious pattern. This situation coincided with the subtropical convergence, where subtropical water (Brasil Current) mixes with cold and low salinity subantarctic water (Falkland Current).

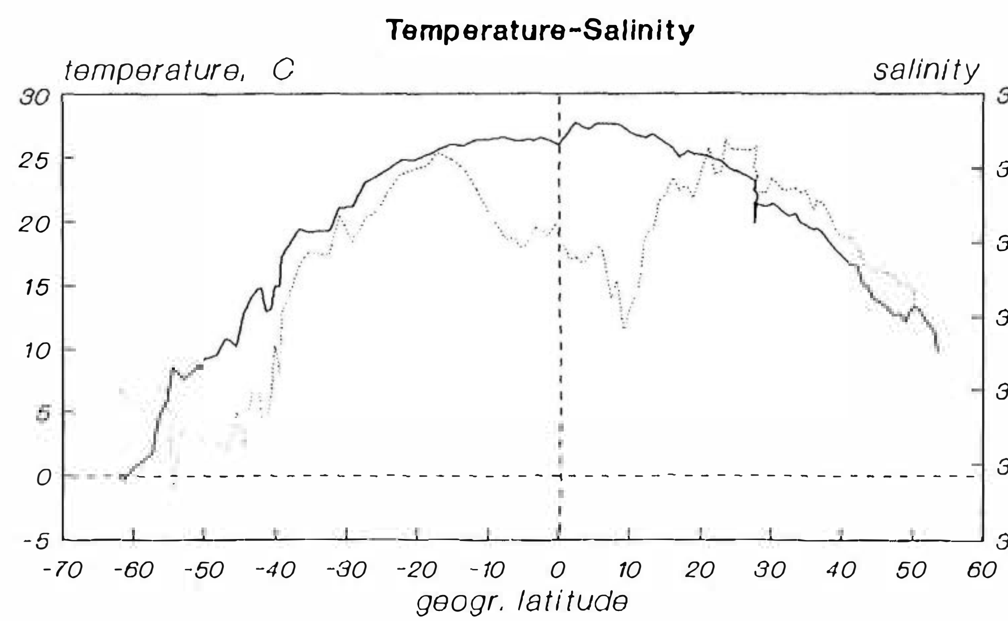


Fig. 2: Temperature (solid linde) and salinity (dotted line) on the N-S Atlantic transect.

Temperature in the temperate zone of the North Atlantic was about 2°C higher compared to temperature of corresponding southern latitudes. This is clearly a seasonal effect of autumn and spring, due to the heat storage capacity of water. In the very south this effect is intensified by the cold water transported by the Antarctic Circumpolar Current. The Equatorial Current system is not well reflected by water temperature.

Inorganic nutrients (Fig. 3): Nitrate and phosphate showed rather similar patterns of distribution over the N-S Atlantic transect. At the beginning of the subtropical zone (about 43°N) both nutrients fell below their detection limit and also in the zone of the equatorial divergence there was no rise in concentrations. There was some increase in concentrations in the south equatorial current, which then decreased nearly to zero at the southern border of the subtropical region. Approaching the continental shelf at 40°S, which coincides with the subtropical convergence at this point, values of nitrate and phosphate increased dramatically. On the shelf there was a pronounced fluctuation in concentrations, probably due to the frontal system of the two dominating currents in this region, the nutrient rich Falkland Current and the poor Brasil Current. After passage of the Drake Passage the values of these two nutrients reached their maximum.

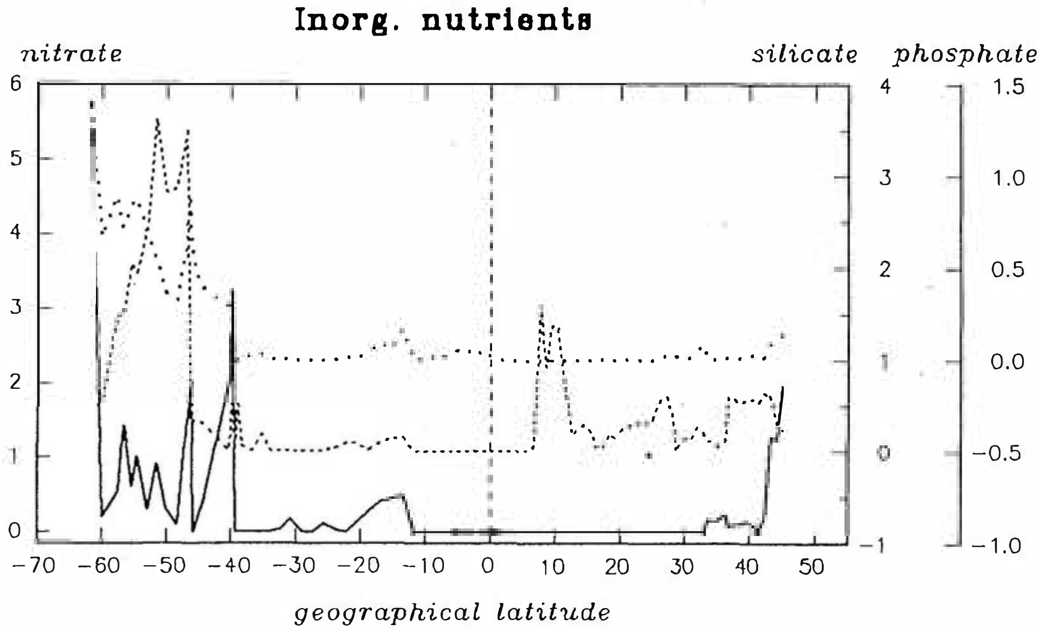
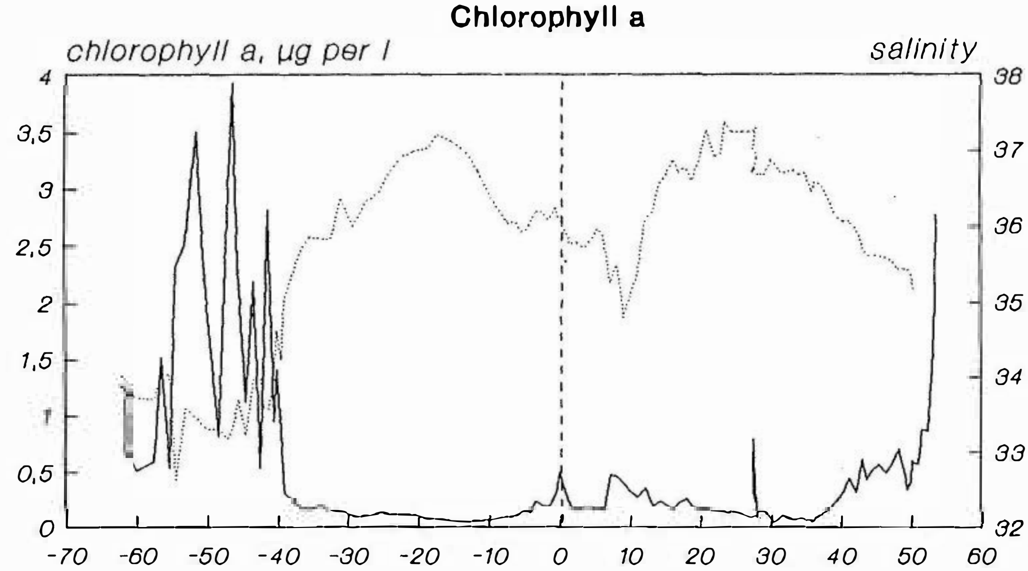


Fig. 3 (a-c): Inorganic nutrients on the N-S Atlantic transect. Scales are in µM l^{-1}. a) nitrate (solid line), b) silicate (short dashed line), c) phosphate (dotted line).

Silicate behaved differently to the former two nutrients. It has to be taken into account, that silicate depends very much on diatom distribution. The two most obvious differences were the strong increase of silicate around 10°N and its distribution on the Patagonean shelf. At 10°N mixing with deeper water and/or input from the atmosphere may be responsible for the increase in concentration. Different from all the other parameters silicate did not show a drastic increase at 40°S, but somewhat further south at 47 °S. The scattering of values on the shelf was not very pronounced and concentrations in the Drake passage were low.



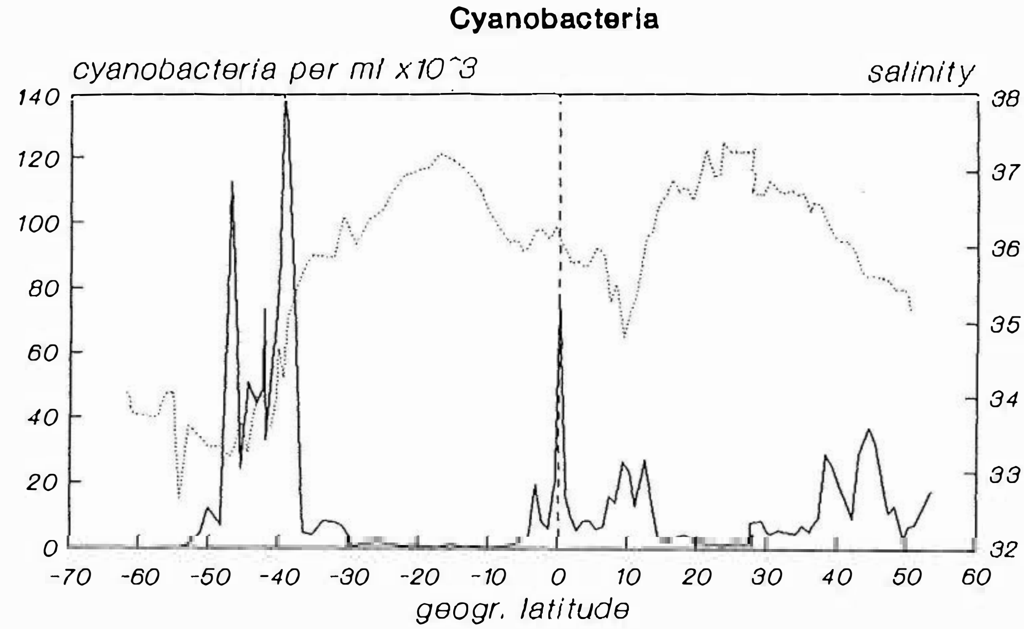


Fig. 4: Chlorophyll a on the N-S Atlantic transect. For better orientation salinity curve is shown in the upper part of the graphs.

Fig. 5: Picocyanobacteria (CB) on the N-S Atlantic transect.

Chlorophyll a (Fig. 4) and Picocyanobacteria (Fig. 5): Phytoplankton biomass, in this study representend by chlorophyll a, reflects the net result of primary production minus losses, such as by grazing, lysis, decomposition and sedimentation. Chlorophyll a was very high in the North Sea coastal area and decreased rapidly towards the subtropical region, where lowest values were measured in the north as well as in the south of the equator.

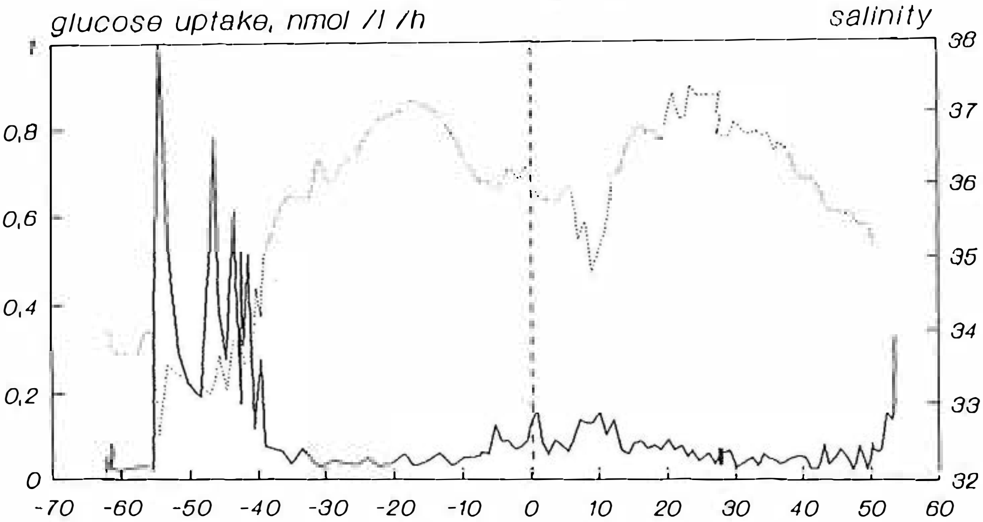
Values increased somewhat in the tropical zone, but they were still low in comparison to those of the moderate climatic zone. As for the other parameters presented above, chlorophyll a concentration showed its highest values on the South American continental shelf. In the Drake Passage (around 60°S) values of chlorophyll a were low, but near the Antarctic peninsula they increased considerably.

The curve of picocyanobacteria (CB) is rather similar to that of chlorophyll a, however, there are some interesting differences between the two variables: CB numbers are not so high in the North Sea and they disappear completely already at the southern region of the Patagonean Shelf. In the Drake Passage and in the Antarctic region no CB were found, although chlorophyll a concentrations remained high. CB increases and peak hights appear to be more pronounced than those of chlorophyll a, especially in the areas west of Spain, around the equatorial divergence zone and at the edge of the South American Shelf (40°S). A comparison with values of primary production of organisms <2 µm shows, that CB are not exclusively responsible for primary production in this size class. Primary production <2 µm may also be high in regions, where CB were not abundant. Microscopical observation revealed, that very small phytoplankton organisms were abundant especially in the subtropical regions, where CB showed their lowest numbers.

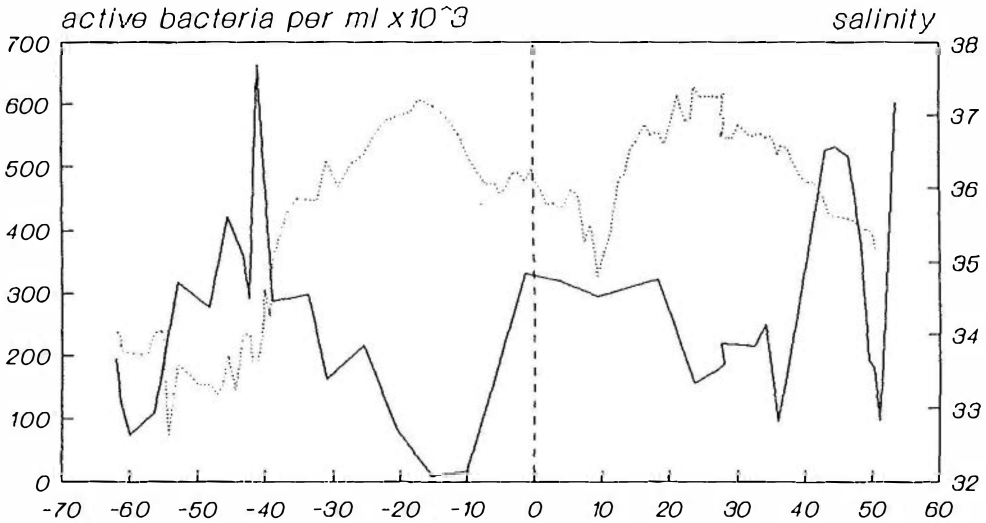
Activities of heterotrophic bacteria: Glucose uptake (Fig. 6), number of active bacteria (Fig. 7) and protease activity (Fig. 8). Taking into acount, that the potential of glucose uptake depends mainly on the numbers of bacteria but also on ambient temperature, variability of this parameter over the N-S Atlantic transect was surprisingly low, with the exception of the Patagonean Shelf area. At first glance bacterial glucose uptake seems to reflect quite accurately chlorophyll a conditions. In detail, there are some differences between the two curves, which suggest different effects of climate and current systems on autotrophic and heterotrophic processes. While chlorophyll a (and also primary production) was generally considerably higher in the moderate climate zone than in the zones of the tropical equatorial current system changes of glucose uptake in these zones were much less pronounced. Also on the Patagonean Continental Shelf, glucose uptake did not increase as strongly as it was found for the chlorophyll a values. In the subtropical areas, glucose uptake did not decrease as much as it was the case for chlorophyll a measurements. Crossing the Drake Passage, glucose uptake decreased dramatically and in the southern polar ice region values increased again slightly.

Numbers of active bacteria (MAR, Fig. 7) were not as frequently measured as the other parameters. This is due to the high amount of radioactivity needed for autoradiography and the overall time demand of the procedure. Therefore, the longitudinal resolution of the active bacteria is much lower than that of the other parameters. Nevertheless, the curve of MAR shows the same characteristics as they have already been pointed out for the other variables. On average active bacteria numbers in the northern coastal regions were about as high as those counted on the Patagonean Shelf, however, it has to be noted, that in the latter area spots on the X-ray film were very much bigger and clustered than in the north. This suggests, that bacteria associated with the southern spring phytoplankton bloom were much more active and/or bigger and/or aggregated than bacteria of the late autumn situation in the north. Also in the tropical zone, somewhat shifted to the north, active bacteria numbers were high, but spot sizes were very small in this area indicating low activity per cell. In the subtropical zones

Glucose uptake



Active bacteria



Protease

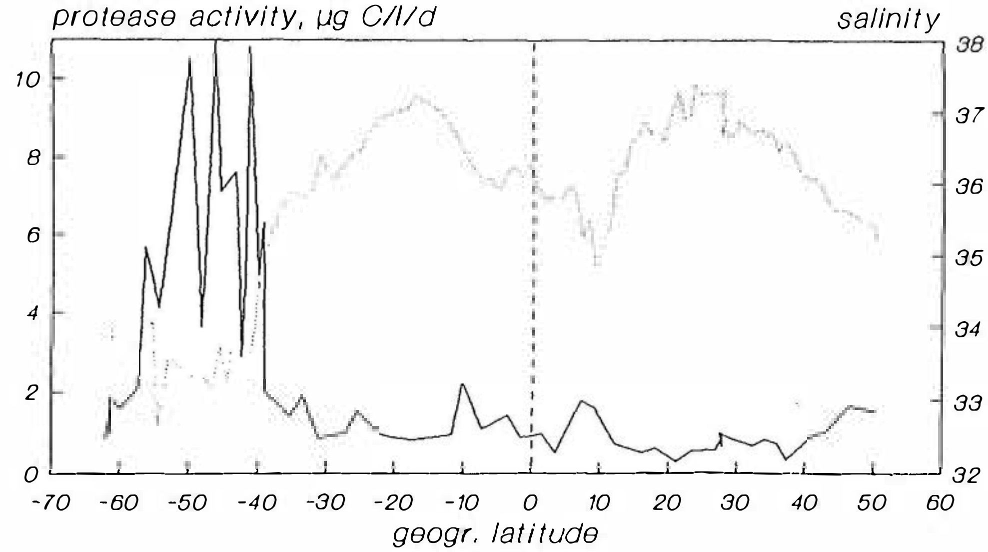


Fig. 6: Glucose uptake potential (V_m glucose) of bacteria on the N-S Atlantic transect.

Fig. 7: Number of active bacteria per ml water (MAR) on the N-S Atlantic transect.

Fig. 8: Extracellular protease activity (EPA) potential of bacteria on the N-S Atlantic transect.

active bacteria numbers were low, but they were comparatively higher in the northern zone compared to the southern zone, which coincides with most of the other microbial activity measurements.

Extracellular protease activity (EPA, Fig. 8) is mainly associated with the bacteria size class (Hoppe 1983, Rosso & Azam 1987), and it has been figured out to be a key factor for bacterial growth (Chrost 1991, Hoppe 1991). Protease potential was relatively low in the northern temperate zone, as it has also been found for heterotrophic glucose uptake. There was a small rise in activity in the tropical equatorial area, but the shift toward more northern latitudes was not observed in this case. On the Patagonean Shelf there was a very strong increase of protease activity, similar to that of heterotrophic glucose uptake. Peaks and minima of protease activity on the shelf coincided in most cases with those of glucose uptake and bacterial growth. In and beyond the Drake Passage, protease activities decreased rapidly, but they were not much lower than those found in much warmer subtropical regions.

Discussion

The N-S Atlantic transect made on the Polarstern Ant X, 1a/b cruise from Bremerhaven to the Antarctic region from Nov. 14h, 1991 to Jan. 2, 1992 harvested a rare set of biological data with a high spatial resolution. The pattern of the different biological parameters studied was rather similar, indicating that there are large scale zones of biological activity, corresponding to distinct hydrographic regions of the Atlantic. On the other hand, there are also differences between the latitudinal patterns of the various physical, chemical, autotrophic and heterotrophic parameters; it is the discussion of these differences, which may help to approach and to understand some fundamental questions in marine microbial ecology:

i) which are the key environmental factors for the development and activity of marine autotrophic and heterotrophic plankton communities in the sequence of global climate zones,

ii) how do these factors influence mass- and activity rate relationships between autotrophic and heterotrophic components in the surface layer of the ocean,

iii) and, how does, in general, the seasonal situation (autumn in the north, spring in the south) influence these relationships (ii) in the Atlantic Ocean?

In detail, there are, of course, many factors and combinations of factors which have an influence on the development and activity of organisms in the surface zone of the ocean, and the number of these factors as well as their combination changes according to investigated spatial and temporal scale dimensions. For events in the ocean factors such as climate, the prevailing current system and distance from land may be considered to be important for the general biological activity.

In our study water temperature serves as a main indicator of the climate and its most obvious influence on organisms in the sea. Currents have not been measured on this N-S Atlantic transect expedition, but their large scale dimensions are well known (Dietrich & Ulrich 1968, Tschernia 1980). Looking closely at the curve of the salinity distribution (Fig. 2), it turns out, that this parameter sufficiently reflects the dominating currents crossed on the N-S transect. Salinity is, of course, also influenced by climatic factors, such as precipitation and evaporation or by ice melting and upwelling events. Nevertheless, salinity can be used to trace the main currents and if other factors influencing salinity can be identified, these are often important for interpretation of biological data.

Biological zones along the transect were established according mainly to salinity characteristics but in some cases zone borders are a compromise of suggestions coming from salinity and biological data (for instance the southern extension of the tropical zone). Base parameters (physical, chemical, phytoplanktological) of biological zones are discussed first and thereof their bacteriological characteristics (Fig. 9 and 10).

Northern temperate zone: North Sea, Channel area, Bay of Biscay (54°-43°N): Chlorophyll a was very high due to eutrophication in the North Sea, unfortunately nutrient measurements were not made there. Chlorophyll a concentration decreased in the Bay of Biscay, but was still quite high (0.5 $\mu g\ l^{-1}$) in comparison to the adjacent subtropical zone). Nitrate with its maximum at the mouth of the Channel (2.3 $\mu M\ l^{-1}$) decreased drastically, phosphate not as much. This was probably due to the input of organic nutrients to the Channel area, which had not been used up by phytoplankton growth in this late season of the year. Silicate on the other hand was low, because it sedimented to depth and had not yet been recycled. Silicate is, relative to phosphate and nitrate, not so much supplied by eutrophied allochthoneous sources.

Northern subtropical zone: Azores Current, Canary Current, North Equatorial Current (43° to about 16°N). Chlorophyll a was very low in this area, picocyanobacteria were quite high at its northern extent and decreased to very low values towards the south. Nitrate and phosphate were still measurable in the vicinity of the Canary Islands (Canary Current). In the North Equatorial Current these nutrients decreased below the detection limit. Silicate obviously did not follow this pattern. This parameter is to much influenced by the specific nutrient requirements of diatom development to reflect general patterns of nutrient consumption and transport.

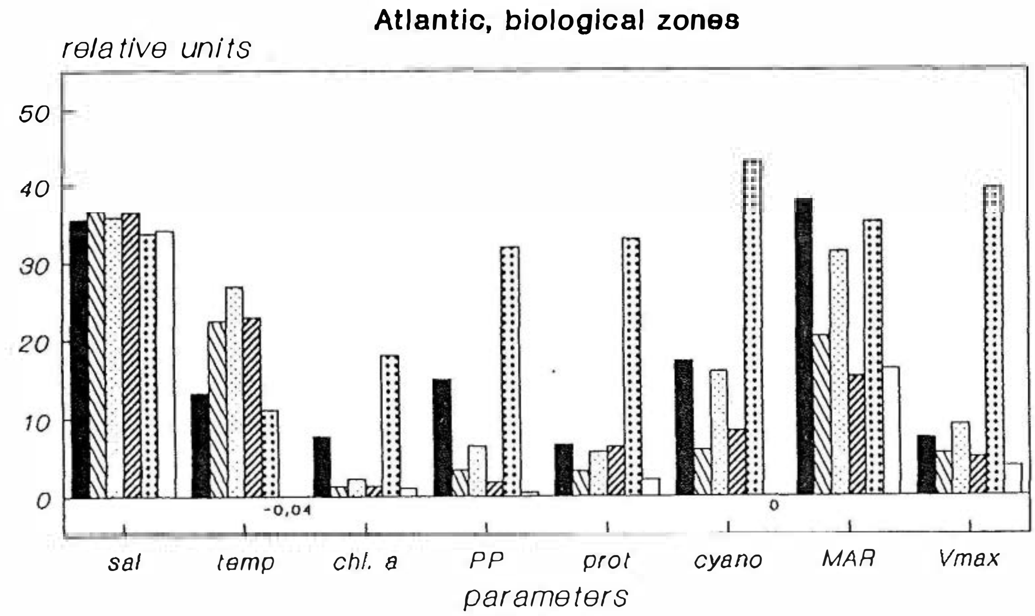
Tropical zone: Equatorial Counter Current, most southern or northern parts, resp., of the Equatorial Currents, Equatorial Divergence and adjacent convergent zones (about 16°N-8°S). In this region the situation changes drastically. Strictly limited to this region, chlorophyll a and picocyanobacteria increase strongly, but not as much as found in coastal areas. Nutrients, with the exception of silicate are low, but not fully depleted. Silicate again does not follow this pattern, showing a very strong increase at the salinity minimum around 10°N. Salinity in this area is well below that of the arid subtropical areas. Several reasons may be responsible for this observation, but it cannot be decided, which one is most important. Heavy rainfall (>2 m y^{-1}) may contribute to salinity decrease at least in the very surface. The current regime in late autumn in this region allows two explanations: the Equatorial Counter Current, which is not very strong during this time of the year (Richardson and Walsh 1986), may have transported mixed Amazonas effluents to this mid ocean position. It is also possible that waters originating from the west African upwelling area (Mittelstaedt 1991), which are low in salinity and originally rich in nutrients, were transported to this part of the tropical zone by the southern band of the north Equatorial Current. The high silicate concentration at the 10°N salinity minimum, where the other nutrients were below the detection limits, is of course puzzling. Chlorophyll a and primary production were not exceptional high at this latitude. Primary production >2 µm was higher than in the adjacent areas, indicating the presence of diatoms. These observations do not agree with the prevailing nutrient situation. Schneider (pers. comm) therefore suggested that the silicate (dust) might have been transported to this mid ocean area via west going winds coming from the African deserts.

Southern subtropical zone: South Equatorial Current, Brasil Current, southern Subtropical Convergence (8°S-40°S). This part of the western South Atlantic is known to have a very low productivity (Dietrich & Ulrich 1968). Chl a concentrations were very low, and so were the numbers of cyanobacteria. Surprisingly, nutrients were abundant in most of the areas affected by the Brasil Current, but their origin could not be detected.

Southern temperate zone: Falkland Current, Patagonean Shelf, Drake Passage (40°S-56°S). The situation changed drastically at the edge of the Patagonean Shelf (40°S, 54°W), which is also the zone of convergence of the Brasil Current and the Falkland Current (Peterson & Stramma 1991). The Falkland Current carries high loads of nutrients and its low temperature and salinity suggest an influence of Antarctic waters. All chemical and biological values were extremely high in this area but they decreased strongly while the ship crossed the Drake Passage and the Antarctic Convergence. Strong patchiness of all variables may be due to subtropical cyclons penetrating this area from the subtropical frontal zone in the north. Note, that higher salinity is often combined with higher temperature. In many cases it is obvious, that these zones are characterized by lower biological values in contrast to surrounding low salinity waters of the Falkland Current.

Antarctic zone: (57°-63°S). Beyond the Antarctic Convergence, in the Bellinghausen and Weddell Sea all biological values, except those of cyanobacteria increased again. Despite of temperatures below 0° C, a spring phytoplankton bloom with relatively high productivity was observed in these shallow coastal areas.

Microbial activity parameters: Velocity of glucose uptake, protease activity, numbers of active bacteria. These parameters follow in principle the latitudinal distribution of primary producers, which in turn is related to the dominating current system and climatic zones of the Atlantic. For better characterization and comparison of the above mentioned zones mean values of the different parameters measured were calculated (Zone specific mean values, Fig. 9). Because sampling along the transect was done at relatively short and constant intervals, zone specifications are believed to be representative.



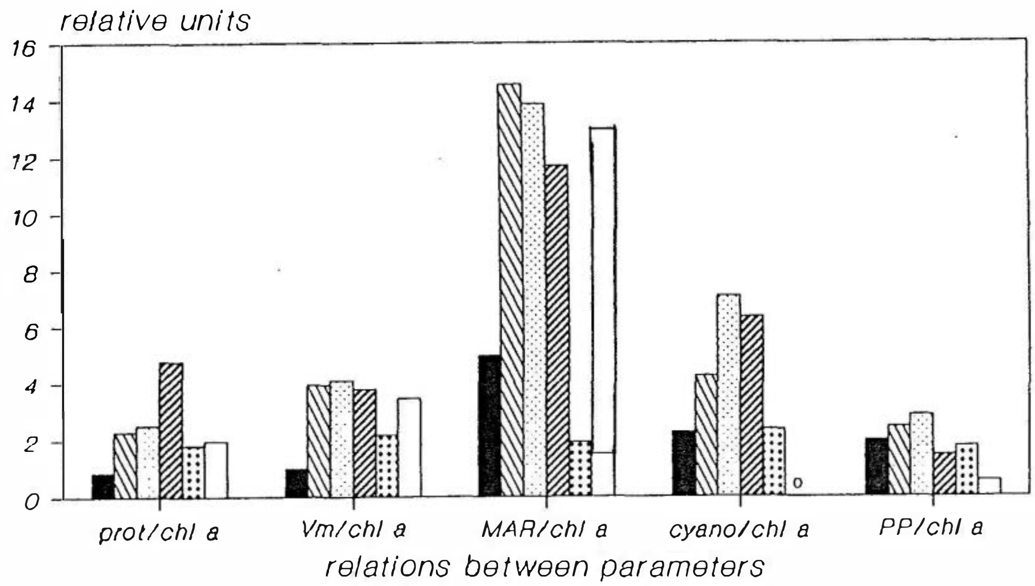


Fig. 9: Mean values of measurements of indicated parameters in latitudinal zones of the Atlantic (zone specific mean values). Zones within one set of columns are from left to right: northern temperate zone (54°N-40°N), northern subtropical zone (40°N-15°N), tropical zone (15°N-5°S), southern substropical zone (5°S-40°S), southern temperate zone (40°S-56°S), antarctic zone (57°S-63°S). sal = salinity, temp = temperature, chl a = chlorophyll a, PP = primary production, prot = protease activity, cyano = picocyanobacteria, MAR = active bacteria, V_m = maximal uptake of glucose.

Fig. 10: Chlorophyll a related zone specific mean values of indicated parameters in latitudinal zones of the Atlantic. Zone characteristics and parameter legend as in Fig. 9.

Most obvious differences between zones exist for the two temperate shelf areas and the warmer zones. However, there are also distinct differences between the two shelf areas, which may be inherent with their special hydrographic situation, but also with seasonal effects. The ratio between the values obtained from the southern and the northern temperate zone (Patagonean Shelf/North Sea, west European Continental Shelf) is 2.4 for chlorophyll a, but 5.3 and 5.1 for glucose uptake and protease activity, respectively. For active bacteria numbers this relationship is nearly 1, but it has to be mentioned, that spot sizes on the X-ray film, which correspond to individual cell activity, were very small in the north but very large in the south.

Certainly the two shelf areas in the temperate zones are not directly comparable. Neverthelessour observations reflect typical autumn/spring situations in such areas. On the Patagonean Shelf we met a late spring situation, in a highly variable region. In some parts of the shelf silicate was low, while nitrate was high and vice versa. Microscopical observation showed snow like aggregations with many embedded algae and bacteria, and detritus particles. Furthermore large diatom cells, which are known for their high exudation of organic matter, were dominating in many places. We conclude from these observations, that the vernal phytoplankton bloom on most parts of the shelf had already exceeded its climax and therefore chlorophyll a (and primary production as well), were relatively low in comparison to extremely high heterotrophic uptake and enzymatic activities. Contrarily, in the northern shelf area of the North Sea and adjacent areas, these bacterial activities were relatively low in comparison to phytoplankton stock and production. The phytoplankton was not blooming, but was still intact. Thus, bacteria were not so much stimulated by this late autumn situation in the north as they were stimulated by algal bloom decay in the south.

In the tropical and the subtropical offshore zones all biological values were lower than on the shelfs. However, if zone specific mean values are normalized to the prevailing chlorophyll a content of the water, the picture changes completely (Fig. 10): Bacterial activities relative to chlorophyll a in the warm regions are frequently 2-4 times higher than on the shelfs of the temperate zone. This is certainly an effect of higher temperatures which stimulate particularly enzyme activity and decomposition, but not so much phytoplankton growth. Values of primary production in relation to chlorophyll a are only slightly higher or even lower in the warmer zones than in the temperate zones (Fig. 10). Moreover, extremely high numbers of active bacteria in relation to chlorophyll may indicate that phytoplankton in the tropics benefits only little from degradation because degraded and incorporated materials remain stored in bacteria or within the microbial loop. It can also be assumed, that cyanobacteria contribute much more to chlorophyll a in the warm nutrient depleted regions of the Atlantic, since up to 85 % of primary production can be attributed to the <2 μm size fraction.

However, the plot of protease activity (and other activities) against temperature does not give evidence for such a strong temperature effect (Fig. 11). Activities remain in a very narrow range over a very wide span of temperatures from minus degrees to 27°C! But on the Patagonean shelf, more characterized by the lower part of the temperature range (5-15 °C), bacterial activities were extremely high, and scattering. As it has been pointed out already, organic nutrient supply on the shelf can be assumed to be high due to plankton bloom decay. This would suggest, that bacterial activities do not depend so much on temperature but on organic nutrient availability. This is clearly a contradiction to the strong temperature effect which may be deduced from Fig. 10.

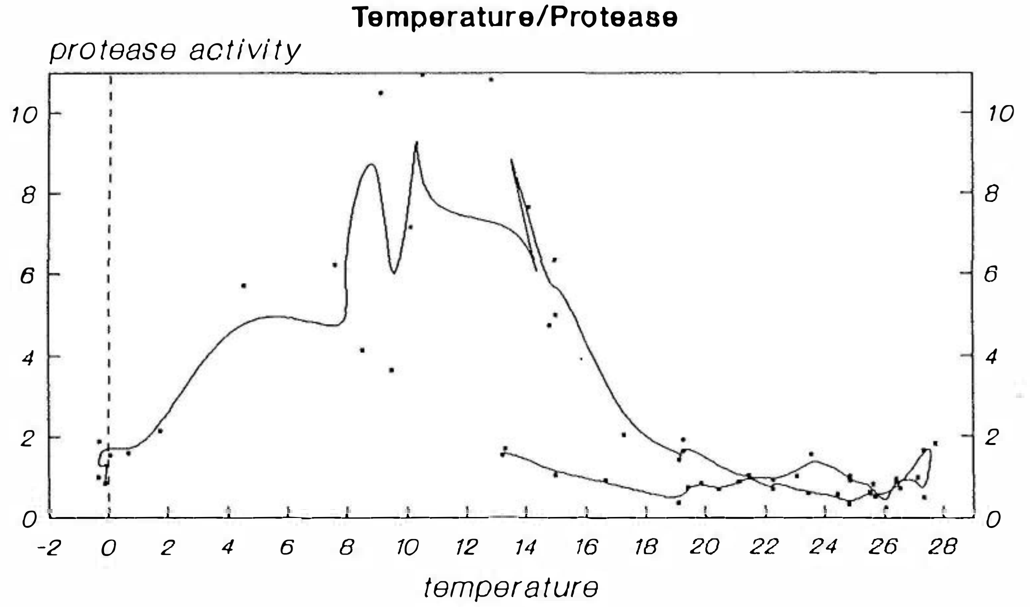


Fig. 11: Protease activity potential related to in situ temperature on the N-S Atlantic transect. The curve begins at about 13 °C (North Sea) and ends at minus degrees in the Antarctic region.

The answer to this paradox probably is, that in the warm regions the stimulating effect of temperature on decomposition processes is compensating the relatively low availability of substrates. Such a system, which is characterized by low primary production and relatively high heterotrophic activity, can only be maintained on the basis of a) small pools of available inorganic and organic nutrients, which favour small organisms and those with active membrane transport mechanisms, b) continuously rapid turnover of the small pools of available nutrients in the surface layer, c) fixation and recycling of elements within the microbial loop, with only little output of inorganic nutrients for the supply of phytoplankton.

On the other hand, on the shelfs in the temperate region bacteria activities in relation to the chlorophyll content are low in comparison to the warm regions. Only the high concentration of available organic nutrients is responsible for high absolute values of bacteria activities on the shelfs (Fig. 10).

It is surprising, that in the very cold Antarctic waters values for bacteria activities in relation to chlorophyll are not much lower than those found in the warmest regions of the ocean or even higher than those of the temperate shelfs. It is still an open question whether nutrient supply alone is responsible for this result or whether an adaptation of bacterial metabolism to low temperatures is also involved. Inspired by investigations in Arctic/Antarctic regions the question of temperature and/or nutrient regulation of marine heterotrophic systems has received increasing attention during the recent years. Bird and Kalff (1984) reported a strong positive empirical relationship between bacterial abundance and chlorophyll concentration in fresh and marine waters. A similar statement, on the basis of bacterial and phytoplankton biomasses was made by Simon et al. (1992). Only in eutrophic environments bacterial abundance was disproportionally low and it was suggested, that instead of stock parameters activity parameters might fit better in these cases. Our investigations show (Fig. 10) that relationships between bacterial activities and chlorophyll a are more variable than those reported for bacterial stocks and phytoplankton.

Measuring ^{3}H-thymidine and ^{3}H-glutamic acid uptake by heterotrophic communities in the Bransfield Strait (Antarctica) Bird and Karl (1988) could not find a direct effect of temperature on uptake rates. Pomeroy and Deibel (1986) observed a suppression of microbial utilization of photosynthetic products at temperatures between -1° and +2° C in Newfoundland coastal waters and, derived from field and enrichment experiments, Pomeroy et al. (1991) hypothesized, that bacterial growth at low temperatures is limited at the cellular physiological level. Our investigations suggest that temperature effects on bacteria metabolism may be compensated by organic nutrient availability to a certain extent.

Lenz (1992) pointed out, that high temperature indirectly favours small cells more than comparatively large ones, and thus the microbial food web dominates in the oligotrophic warm water regions. Cold water ecosystems are more dominated by the "classical" food chain, which is based on the grazing activity of herbivorous zooplankton. We agree with the general validity of Lenz' statements, however, it should be pointed out that in reality bacterial activity is by far not as low in cold waters (or high in subtropical waters), as it would be expected from van't Hoff's law. Of course, our measurements from the temperate and cold zones provide only a momentary picture, strong annual variations can be expected there. As summed up by Lochte et al. (1993) for the JGOFS pilot study temporal variations of plankton stocks and activities during the vernal plankton succession may be as large as the regional variation observed by us over the whole Atlantic transect.

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